The Tribal Position of *Hypocalyptus* Thunberg (Fabaceae)

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ABSTRACT. The tribal position of *Hypocalyptus* Thunberg in the Fabaceae subfamily Papilionoideae is investigated. A phylogenetic analysis in which the Australian Bossiaeeae and Mirbelieae, African Podalyrieae and Crotalarieae, South American Sophoreae and Millettieae, and northern temperate Thermopsideae and Genisteae are included, indicates that there is no direct relationship between *Hypocalyptus* and any of the tribes. It is therefore proposed that the monotypic subtribe Hypocalyptinae Yakovlev be raised to tribal level as Hypocalypteae (Yakovlev) A. L. Schutte. A description of the tribe is presented, followed by an enumeration of the three species recognized.

Hypocalyptus Thunberg is a genus of papilionoid legumes confined to the Cape Floristic Region of South Africa. The genus is easily recognized by its trifoliolate leaves, magenta-pink flowers with a yellow nectar guide, intrusive calyx base, and fused stamens. It comprises three distinct species, which are restricted to the fynbos vegetation of the Western and Eastern Cape Provinces (Dahlgren, 1972).

Despite its well-defined generic circumscription, the tribal affinities of *Hypocalyptus* have been uncertain ever since Bentham's (1837, 1839) fundamental classification of the subfamily was published. This is clearly reflected in the number of times the genus has been transferred from one tribe or subtribe to another. Bentham (1837, 1839, 1844) placed the genus in the tribe Loteae subtribe Genistinae, which he later changed to the tribe Genisteae subtribe Cytisinae (Bentham, 1865). Harvey (1862) retained the genus in the Genisteae, recognizing no subtribes. In 1964 Hutchinson raised the Cytisinae to tribal level and allocated *Hypocalyptus* to the Cytiseae. Polhill (1976, 1981f) transferred the genus to the tribe Liparieae, which Yakovlev (1991) subdivided into the subtribes Lipariinae and Hypocalyptinae. He placed *Hypocalyptus* in the monotypic Hypocalyptinae. The problem regarding the tribal position of *Hypocalyptus* is thus quite evident. This has, in fact, also been pointed out by several authors (Dahlgren, 1972; Polhill, 1976, 1981e, 1994; Goldblatt, 1981; Bell et al., 1978; Van Wyk et al., 1994; Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).

As part of a taxonomic study of the tribes Podalyrieae and Liparieae, Schutte (1995) investigated the position of *Hypocalyptus* within the tribes. Morphological, anatomical, cytological, and chemical characters were examined and analyzed cladistically to determine inter- and infratribal relationships. The results clearly indicated that *Hypocalyptus* is misplaced in the Liparieae and should be excluded, while the Podalyrieae and remainder of the Liparieae are monophyletic and should be united (Schutte, 1995; Schutte & Van Wyk, 1997).

Hypocalyptus deviates from the Podalyrieae (including the Liparieae) in no less than nine critical characters (Table 1). Of particular interest are the micromorphological characters, i.e., floral pigmentation (Van Wyk et al., 1994); the accumulation of canavanine in the seed (Bell et al., 1978); a chromosome base number of $x = 10$ (Goldblatt, 1981; Van Wyk & Schutte, 1995); and ephemeral antipodals in the female gametophyte (Schutte, 1997). These, in addition to the five macromorphological characters of the stamens, seed, and pods, indicate unambiguously that *Hypocalyptus* does not fit in the Podalyrieae.

The aim of this paper is to examine the phylogenetic position of *Hypocalyptus* within the subfamily Papilionoideae. To this end we scanned the literature and selected all the tribes which are assumed to, or have previously been suggested to, be possibly related to the genus. Based on these criteria, the Australian Bossiaeeae and Mirbelieae, African Podalyrieae and Crotalarieae, northern temperate Genisteae and Thermopsideae, and South American Sophoreae and Millettieae were chosen as outgroups (see, e.g., Dahlgren, 1972; Polhill, 1976, 1981a, 1981g, 1994; Crisp & Weston, 1987). It is important to note that the primary objective of this study is to establish whether *Hypocalyptus* is directly related to any of the tribes, and not to analyze the relationships among the different tribes.

Table 1. Taxonomic differences between *Hypocalyptus* and the tribe Podalyrieae.

Character	Podalyrieae	*Hypocalyptus*
1. Stamen fusion	free to open sheath	closed tube
2. Seed aril shape	interrupted at the micropylar end	continuous around the hilum
3. Micropyle type	punctate	y-shaped
4. Micropyle position	within hilar region	outside hilar region
5. Pods	sessile	stipitate
6. Chromosome base number	$x = 9$	$x = 10$
7. Antipodals	persistent	ephemeral
8. Floral pigments	esters of cyanidin-3-glucoside	malvidin-3-glucoside
9. Canavanine	absent	present

Analysis and Results

The data matrix, characters, and character states used for the tribal analysis are given in Table 2. These have largely been taken from Van Wyk and Schutte (1995), with some additions and alterations, e.g., the inclusion of *Hypocalyptus* as a separate taxonomic unit, the incorporation of the Millettieae and the omission of the *Argyrolobium* group (now included in the Genisteae; Van Wyk & Schutte, 1995). Data for the Australian Bossiaeeae and Mirbelieae came mainly from Polhill (1976, 1981c, 1981d) and Crisp and Weston (1987, 1995). Information on the Millettieae and Sophoreae has been taken from Geesink (1981) and Polhill (1981b), respectively. Polhill (1976) and Bisby (1981) were consulted for information on the Genisteae, and Turner (1981) for data on the Thermopsideae. Variation in the characters and polarization of character states are discussed in the references given at the end of each character. Where plesiomorphic and apomorphic states co-occur, the taxon was scored for the plesiomorphic state. Autapomorphies for the taxa were excluded from the analyses, since they serve no purpose as grouping characters.

The computer software package Hennig 86 (Farris, 1988) was used for the cladistic analysis and the "mhennig*", "bb*", and "ie" algorithms were applied to produce cladograms of minimal length. A single, fully resolved topology resulted from the analysis, with a length of 24, a consistency index of 66, and a retention index of 71 (Fig. 1). The result shows that *Hypocalyptus* has no direct relationship with the Podalyrieae, the Australian tribes, or the Millettieae and Sophoreae.

Discussion

Hypocalyptus remains a perplexity as far as its taxonomic position is concerned. It has a unique combination of characters, but the individual characters are shared with a wide range of different tribes. The intrusive calyx is shared with the Podalyrieae; the closed stamen tube is shared with the Millettieae and Genisteae; a fleshy aril is present also in the Podalyrieae, Bossiaeeae, Mirbelieae, and some Millettieae; a Y-shaped micropyle situated outside the hilum occurs also in the Sophoreae and Millettieae, and the presence of canavanine is shared with the Bossiaeeae, Mirbelieae, and Millettieae.

Clearly, *Hypocalyptus* seems to fit neither in the Podalyrieae, nor the Sophoreae, nor the Australian Bossiaeeae or Mirbelieae. Even the Millettieae, with which it shares a number of characters, deviate in having complex pseudoracemose inflorescences and diadelphous or pseudomonadelphous stamens, with two fenestrellae at the base of the stamen tube. Furthermore, in this tribe a nectar disk is generally present, and chemical compounds, such as pterocarpans, arylcoumarins, and rotenoids, are produced (Geesink, 1981; Sousa & Pena de Sousa, 1981). None of these characters have been located in *Hypocalyptus*.

Despite the mentioned similarities, there is no convincing evidence to support a direct link between *Hypocalyptus* and any of the investigated tribes. In the past, several eminent scientists (e.g., Bentham, Polhill, Dahlgren), with vast insights into relationships in the Papilionoideae, have allocated *Hypocalyptus* to various tribes, but have consistently found it to be an odd genus with no obvious relationships. We therefore conclude and propose that the genus be assigned separate tribal status and perhaps be placed near the Millettieae, with which it shows signs of a possible affinity. In 1991, Yakovlev placed *Hypocalyptus* in a monotypic suprageneric group, but we propose tribal status, rather than subtribal status within the Podalyrieae, as the genus has no direct affinity with the Podalyrieae. An independent tribal position would emphasize the anomalous character combinations in

Table 2. Characters and character states used for the cladistic analysis of *Hypocalyptus* and the tribes Sophoreae, Millettieae, Podalyrieae, Mirbelieae, Bossiaeeae, Crotalarieae, Genisteae, and Thermopsideae. The fully resolved cladogram generated from this data set is shown in Figure 1.

Taxa	Character states			
Sophoreae	00000	00000	00000	0
Bossiaeeae	00101	0110?	?1001	0
Crotalarieae	10000	10001	10100	0
Genisteae	10110	10011	10110	1
Hypocalyptus	11100	00100	00001	1
Millettieae	00000	00000	00001	1
Mirbelieae	00101	01101	11001	0
Podalyrieae	01100	10101	10100	0
Thermopsideae	10110	000??	??110	0

Characters

1. Leaf type: pinnate, at least in some taxa (0); digitate or simple (1) (Polhill, 1981a; Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
2. Calyx base: not intrusive (0); intrusive in most taxa (1) (Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
3. Calyx upper lobes: not fused higher up (0); fused higher up to form an upper lip (1) (Polhill, 1981a; Van Wyk & Schutte, 1995).
4. Calyx lower lobes: not fused higher up (0); fused higher up to form a trifid lower lip (1) (Polhill, 1981a; Van Wyk & Schutte, 1995).
5. Corolla: without red guide marks (0); yellow with red guide marks (1) (Crisp & Weston, 1987; Van Wyk & Schutte, 1995).
6. Anther dimorphism: not dimorphic or slightly dimorphic (0); storngly dimorphic (1) (Polhill, 1981a; Van Wyk & Schutte, 1995).
7. Anther connective: narrow (0); broad and dark colored (1) (Crisp & Weston, 1987).
8. Seed aril type: non-fleshy (0); fleshy (1) (Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
9. Seed aril shape: without a tongue-like extension (0); with a tongue-like extension (1) (Van Wyk & Schutte, 1995).
10. Seed micropyle type: ypsaloid (0); punctate (1) (Manning & Van Staden, 1987; Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
11. Seed micropyle position: outside the hilum (0); inside the hilum or on the rim (1) (Manning & Van Staden, 1987; Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
12. Giant antipodal cells: absent (0); present, at least in some taxa (1) (Crisp & Weston, 1995; Schutte, 1997).
13. Quinolizidine alkaloids: absent in most taxa (0); present in most taxa (1) (Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
14. α-Pyridone alkaloids: absent in most taxa (0); present in most taxa (1) (Van Wyk & Schutte, 1995).
15. Canavanine: absent (0); present, at least in some taxa (1) (Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).
16. Stamens: free or fused into an open tube (0); fused into a closed tube (1) (Polhill, 1981a; Van Wyk & Schutte, 1995; Schutte & Van Wyk, 1997).

Hypocalyptus and indicate its incongruous position within the subfamily. The necessary taxonomic change is presented below, with a description of the tribe and a list of the species recognized.

Tribe **Hypocalypteae** (Yakovlev) A. L. Schutte, stat. nov. Based on: Liparieae (Bentham) Harvey subtribe Hypocalyptinae Yakovlev, Bobovye Zemnogo Shara, 87. 1991.

Tall erect shrubs or sprawling subshrubs. Leaves alternate, palmately trifoliolate, petiolate; leaflets oblanceolate to broadly obovate, mucronate, flat; stipules linear. Inflorescences terminal, racemose, 2–50-flowered. Bracts linear to lanceolate, sometimes laterally denticulate, usually caduçous. Bracteoles linear to lanceolate. Calyx intrusive at base; upper two lobes fused higher up than lower three lobes; carinal lobe as long as the other lobes. Corolla violet, mostly with a yellow nectar guide on the standard petal, glabrous. Standard ovate to circular; apex emarginate or mucronate. Wing petals longer than the keel, elongate, rounded, with the apical part much widened, auriculate; petal sculpturing present. Keel petals semicircular, with a small pocket; apex shortly to strongly beaked. Stamens 10, filaments fused into a closed tube; anthers slightly dimorphic, alternately dorsifixed and basifixed. Pistil stipitate; ovary glabrous, 3–30-ovuled; style curved upward, glabrous. Pods chartaceous, linear, oblong or ovate, laterally compressed or inflated, stipitate, beaked; 5–6-seeded. Seeds obovate, reniform or oblong; hilum elliptic; aril fleshy, collar-like, continuous around the hilum. Chromosome number $2n = 20$. 1 genus with 3 species.

The synopsis presented here has been taken from Dahlgren's (1972) revision of the genus. Full synonymy of the species recognized is not reiterated here.

Hypocalyptus Thunberg, Prod. Pl. Cap., 124. 1800. TYPE: *Hypocalyptus sophoroides* (P. J. Bergius) Baillon.

Crotalaria L. sect. *Purpureae* Bentham, in Hooker, Lond. J. Bot. 2: 590. 1843. TYPE: *Crotalaria purpurea* Ventenat [= *Hypocalyptus coluteoides* (Lamarck) Dahlgren].

Loddigesia Sims, in Curtis's Bot. Mag. 24: 965. 1806. TYPE: *Loddigesia oxalidifolia* Sims [= *Hypocalyptus oxalidifolius* (Sims) Baillon].

1. **Hypocalyptus sophoroides** (P. J. Bergius) Baillon, Hist. Pl. 2: 336. 1870. *Spartium sophoroides* P. J. Bergius, Descr. Pl. Cap., 141. 1767. TYPE: Without locality, *Anon. s.n.* (holotype, SBT).

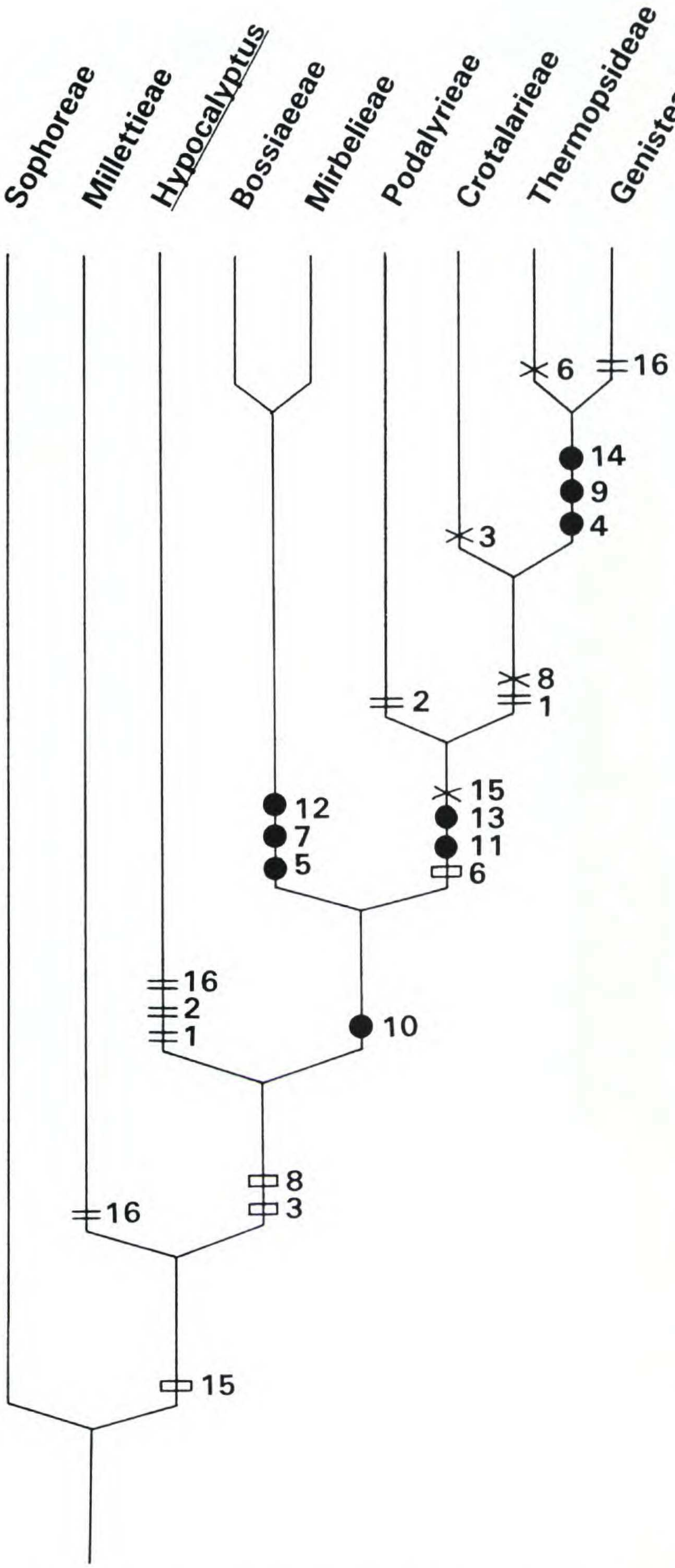

Figure 1. Fully resolved cladogram of relationships at the tribal level, based on the data set in Table 2. Dot, an apomorphy without homoplasy; open box, an apomorphy with subsequent reversal; =, a convergence; x, a reversal.

2. **Hypocalyptus coluteoides** (Lamarck) Dahlgren, in Bot. Not. 125: 108. 1972. *Crotalaria coluteoides* Lamarck, Encycl. 2: 200. 1786. TYPE: Without locality, *Anon. s.n.* (holotype, P-LAM).
3. **Hypocalyptus oxalidifolius** (Sims) Baillon, Hist. Pl. 2: 336. 1870. *Loddigesia oxalidifolia* Sims, Curtis's Bot. Mag. 24: 965. 1806. TYPE: "*Loddigesia oxalidifolia*," plate 965. 1806. (iconotype).

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